

## Review

# The ichthyotoxic genus *Pseudochattonella* (Dictyochophyceae): Distribution, toxicity, enumeration, ecological impact, succession and life history – A review



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## ABSTRACT

The marine genus *Pseudochattonella* is a recent addition to the list of fish killing microalgae. Currently two species are recognised (viz. *P. verruculosa* and *P. farcimen*) which both form recurrent coastal blooms sometimes overlapping in space and time. These events and their ecological and economic consequences have resulted in great interest and concern from marine biologists and the aquaculture industry. Since the first recorded blooms in Japanese (late 1980s), Scandinavian (1993) and Chilean (2004) waters numerous studies have focused on understanding the causative means of the fish killing. Mortality is probably due to *Pseudochattonella* discharging mucocysts that cause gill irritation and damage to the fish kills. Here, a review is provided of the literature on *Pseudochattonella* that covers the last ca. 25 years and focus on a number of topics relevant to understanding the general biology of the genus including ways to distinguish the two species. The literature addressing biogeography and known harmful events is evaluated and based on these findings an updated distribution map is proposed. *P. farcimen* is presently restricted to North European waters. Despite being very difficult to delineate based on morphology alone the two *Pseudochattonella* species seem to have separate growth optima. In laboratory experiments *P. verruculosa* consistently has higher temperature growth optima compared to *P. farcimen* though periods of overlap have been noted in the field. The review ends by proposing five areas with knowledge gaps and each of these could form the basis of future studies.

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## 1. Introduction

The ichthyotoxic genus *Pseudochattonella* (Dictyochophyceae) is a marine heterokont phytoflagellate currently comprising two species (viz. *P. farcimen* and *P. verruculosa*). *Pseudochattonella* forms recurrent extensive blooms in coastal waters in Japan, New Zealand and Northern Europe (Baba et al., 1995; MacKenzie et al., 2011; Naustvoll et al., 2002). Recently the causative microalga for fish kill in Chile was identified to be *P. cf. verruculosa* (Alejandra Aguilera, personal communication). Blooms of *Pseudochattonella* spp. have proved to be extremely damaging to fish not only those in intensive aquaculture systems but also wild stocks (Andersen et al., 2015). Fish mortalities of caged fish such as Atlantic salmon (*Salmo salar*) resulted in substantial financial losses to the aquaculture industry as well as impacting the marine ecosystem as a whole (Naustvoll, 2010; Clement et al., 2016). The mechanism of toxicity is yet unknown but the most common mode of action is by acute gill irritation and damage to the fish gills, reducing gas exchange efficiency (MacKenzie et al., 2011; Andersen et al., 2015). Here the literature surrounding the current biology of *Pseudochattonella*, one of the most recently added phytoflagellates to the list of harmful algal bloom (HAB) species is reviewed. The review is based on studies conducted over a period of ca. 25 years. The review ends with a proposal for the direction of future studies of *Pseudochattonella* to address some of the knowledge gaps uncovered.

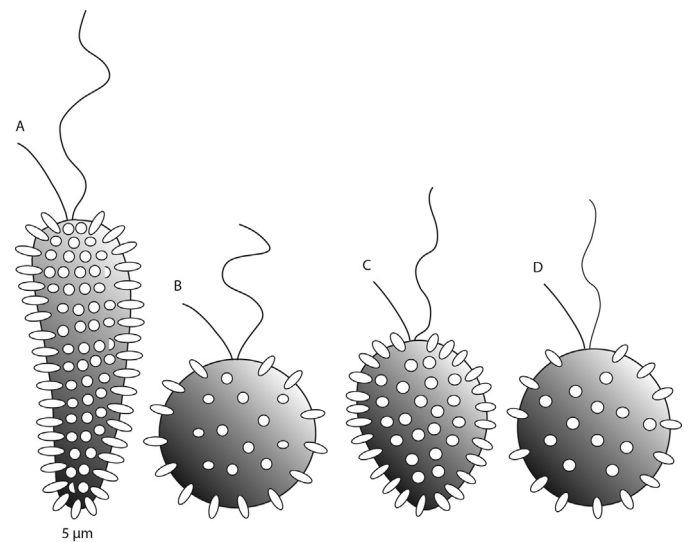
## 2. Morphological characteristics and species identity

Both species of *Pseudochattonella* possess a variable morphology with size and form changing in response to growth phase and growth conditions (personal observations) making them virtually impossible to delineate to species level. Cell shape ranges from long allantoid to conical shaped and oval or small spherical cells (Fig. 1). These can occur with or without numerous mucocysts that when present are often evenly distributed giving the cell surface a warty-like appearance. Smaller spherical cells are often smooth. Elongated cells vary between 12–34  $\mu\text{m}$  in length and 4–9  $\mu\text{m}$  in width. Oval cells are approximately 14  $\mu\text{m}$  long and 10  $\mu\text{m}$  wide whereas smaller spherical cells are ca. 5  $\mu\text{m}$  in diameter (Edvardsen et al., 2007). Spherical cells were observed to aggregate at the bottom of cell culture flasks, suggesting that they are less motile. Elongated cells contain 30–35 golden-brown chloroplasts (Edvardsen et al., 2007). Two heterokont flagella are present; a long anteriorly directed flagellum, which can range from 9 to 20  $\mu\text{m}$  in length is used to pull the cell forward, while a shorter less obvious flagellum faces backwards. The mucocysts when present protrude outwards and vary in size and shape from oval to pointed, oblong and elongated. The peripheral mucocysts often discharge on fixation leaving an empty pocket and making identification using light microscopy difficult (Edvardsen et al., 2007; Jakobsen et al., 2012). Mucus secretion can be discharged laterally or posteriorly from the mucocysts forming tails. Some mucocysts have been observed to form chains (Chang et al., 2014). Small but marked

differences can be observed when comparing the shape of the nucleus in thin-sectioned material examined under a transmission electron microscope (TEM). The nucleus of *P. verruculosa* is rounded whereas it is branched in *P. farcimen*. Subtle species-specific differences also exist in the morphology of their flagella hairs (Edvardsen et al., 2007).

## 3. Taxonomy

The taxonomic history of both species of *Pseudochattonella* (Y. Hara & Chihara) Hosoi-Tanabe, Honda, Fukaya, Inagaki & Sako has been in a state of flux. Originally the type species (viz. *P. verruculosa*) was described as *Chattonella verruculosa* Y. Hara et M. Chihara but it possessed certain features not present in the genus *Chattonella* B. Biecheler including the protruding mucocysts, the discoid chloroplast with embedded pyrenoids invaded by 1 or 2 canals and the absence of osmiophilic particles in the peripheral cytoplasm (Hosoi-Tanabe et al., 2007). Additionally a phylogenetic analysis based on nuclear-encoded SSU rDNA revealed that it clustered with members of the order Dictyochales within the class Dictyochophyceae. Hence, the genus *Pseudochattonella* was proposed for *P. verruculosa* (Y. Hara & M. Chihara) S. Tanabe-Hosoi, D. Honda, S. Fukaya, Y. Inagaki & Y. Sako making *Chattonella verruculosa* a synonym. One month later Edvardsen et al. (2007) suggested the new genus *Verrucophora* Eikrem, Edvardsen & Throndsen for *V. farcimen* Eikrem, Edvardsen & Throndsen and showed it to form a sister taxon to *P. verruculosa* in a phylogenetic analysis based on nuclear-encoded SSU rDNA. Due to reasons of priority (ICBN, Article 31) *V. farcimen* is now considered a synonym of *Pseudochattonella farcimen* (W. Eikrem, B. Edvardsen,



**Fig. 1.** Schematic drawings of *Pseudochattonella farcimen* (A, B) and *Pseudochattonella verruculosa* (C, D). (A, B) Two of the cell morphologies (elongate and small round shape). (C, D) Two of the cell morphologies (droplet and round shape). Numerous mucocysts are distributed on the surface of the cell.

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